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Research

Fidelity and Timing of Spotted Lanternfly (Hemiptera: Fulgoridae) Attack Patterns on Ornamental Trees in the Suburban Landscape

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Abstract

Invasive herbivores can have dramatic impacts in new environments by altering landscape composition, displacing natives, and causing plant decline and mortality. One of the most recent invasive insects in the United States, the spotted lanternfly (*Lycorma delicatula*), has the potential to cause substantial economic and environmental impacts in agriculture and forestry. Spotted lanternfly exhibits a broad host range, yet reports of late-season movement from the surrounding landscapes onto select tree species in suburban environments have been reported. In this study, we aimed to evaluate the fidelity of spotted lanternfly attack on specific, individual trees within the same species during this movement period. In 2018 and 2019, we observed that individual red (*Acer rubrum* L. [Sapindales: Sapindaceae]) and silver maple (*Acer saccharinum* L. [Sapindales: Sapindaceae]) trees were preferentially attacked over other nearby trees of the same species. Foliar elemental composition was a good predictor of spotted lanternfly attack numbers, indicating that individual variation in nutrients may influence spotted lanternfly attraction to and/or retention on maple trees. Our data also confirm reports of late-season movement from surrounding landscapes throughout autumn. Collectively, our results show that spotted lanternfly exhibits some fidelity to particular trees in the landscape during this movement period. While other potential mechanisms also contribute to host plant selection by spotted lanternfly, our data show that host nutritional profiles influence spotted lanternfly infestation of suburban trees at the landscape scale. Our data establish that late-season infestations of suburban trees by spotted lanternfly occurred and that variation in host quality should be further considered in the management of this invasive insect pest.

Key words: forestry, Hemiptera, invasive species, maple, silviculture

Introduction of herbivorous insects into novel habitats has dramatic consequences for ecosystem functioning (Kenis et al. 2009, Bradshaw et al. 2016). In some instances, naïve hosts lack immediate and adequate resistance against novel attackers, resulting in rapid mortality and changes in landscape composition (Jenkins et al. 1999, Gandhi and Herms 2009, Villari et al. 2016). In other cases, impacts of invasive species may manifest over longer periods of time (Strayer et al. 2006). A myriad of factors influence the ways in which plants are used and colonized by novel invaders, and understanding patterns of host plant selection, especially for polyphagous herbivores, is important for predicting how invasive insects will select hosts in novel environments.

The spotted lantern fly, *Lycorma delicatula* (Hemiptera: Fulgoridae), is a new invader in the United States, first detected in September 2014 in eastern Pennsylvania. Prior to arriving to the United States, spotted lanternfly had been detected as an invasive species in Korea in 2004 (Han et al. 2008), where it was reported to cause economic damage to grape, apple, and stone fruit (Lee et al. 2019). Efforts to eradicate spotted lanternfly in the United States have thus far been unsuccessful. Currently, 26 counties in Pennsylvania, as well as portions of Delaware, Maryland, New Jersey, Virginia, and West Virginia are under quarantine. Spotted lanternfly has the potential to inhabit many regions of United States beyond its current detectable range (Jung et al. 2017, Wakie et al. 2020), suggesting that widespread establishment of this invasive pest is possible. A phloem-feeding insect, spotted lanternfly has demonstrated the potential to cause substantial impacts to its host plants. Specifically, vineyards infested with spotted lanternfly have reported as much as 90% yield loss, as well as loss in fruit quality, and increased winter mortality (Urban 2020).

Spotted lanternfly boasts a broad host range, feeding on over 70 plant species (Dara et al. 2015). Generally, spotted lanternfly does not appear to occupy a singular feeding source for the duration of its development (J.M.U., personal observations). As early instar (first to third) nymphs, spotted lanternfly feeds on herbaceous plants and the fleshy portions of woody plants. Fourth instar nymphs are commonly observed feeding on woody plant tissues, and seem to narrow their host use, being most frequently observed on black walnut (*Juglans nigra* Linnaeus [Fagales: Juglandaceae]) and tree of heaven (*Ailanthus altissima* (Mill.) Swingle [Sapindales: Simaroubaceae]) (Liu 2019, Urban 2020). All nymphal instars and adults are also reported to feed upon wild and cultivated grapes (*Vitis* spp.) through the growing season (Leach and Leach 2020). Adults feed on a diversity of trees through late-summer months. Observations in Pennsylvania suggest that black walnut, tree of heaven, grapes, maples (*Acer* spp.), willow (*Salix* spp.), and birches (*Betula* spp.) are among the preferred hosts of late instar and adult spotted lanternfly. However, preference for a particular tree species largely depends upon the availability of hosts in a given area, making it challenging to predict where spotted lanternfly will occur in high numbers.

A factor that further contributes to the unpredictability of spotted lanternfly infestations and densities in the landscape is this pest's mobility. Beginning in September, spotted lanternfly becomes increasingly active and exhibits a 'flight' or 'swarming' behavior (Baker et al. 2019, Myrick and Baker 2019). During this period, spotted lanternfly have been observed flying, often in high numbers, to new and previously uninfested areas (Urban 2020). This behavior occurs through October, and during this time, spotted lanternfly appears to heavily feed and become reproductively mature, having increased body mass (J. M. Urban, unpublished data) and expansion of yellow areas of the abdomen (Wolfin et al. 2019). This time period is critical to management, as these movements correspond to increased populations on previously uninfested grapes in commercial vineyards as well as ornamental trees in suburban landscapes (Leach and Leach 2020, Urban 2020). During this late-season movement, there have been many anecdotal reports of spotted lanternfly arriving to and feeding upon ornamental trees in unusually high numbers, while other trees of the same species in close proximity remain essentially free of spotted lanternfly infestation. In preliminary observations, spotted lanternfly abundances on neighboring trees can differ by three orders of magnitude (B.W., personal observations).

The phenomenon of thousands of spotted lanternfly feeding upon, and seemingly showing high preference for specific trees in a landscape is somewhat unique to spotted lanternfly outbreaks in the invasive range. However, a similar phenomenon has also been reported for other species of Fulgoridae in their native range. Many tropical and subtropical species of Fulgoridae are often very challenging to locate (J. M. Urban, unpublished observation) and are represented in collections as singletons despite being highly colorful and sometimes exhibiting charismatic morphologies. There have been some reports of tropical Fulgoridae showing preference, or high fidelity to specific trees, over others throughout a given landscape (Hogue 1984; O'Brien 2002; Goemans 2006). For example, Hogue (1984) reports visiting trees identified by tour guides in the Peruvian rain forest upon which the fulgorids *Lystra lanata* (Hemiptera: Fulgoridae) and *Fulgora* spp. can be consistently found, often in high numbers. O'Brien (2002) reports similar observations, including that fulgorids (e.g., *Enchophora sanguinea*) show high fidelity to specific trees over years or decades at La Selva, Costa Rica. In Gunung Mulu National Park in Sarawak, Malaysia, guides often know the location of 'fulgorid trees' and include them in tours given to visitors (J. M. Urban, unpublished). On three particular trees (in three different species in two families) at this National Park, ~80 individuals of *Penthicodes farinosa* (Hemiptera: Fulgoridae) were live-collected and marked for observation (J. M. Urban, unpublished), representing an unusually high density of an otherwise cryptic species.

Little is known about the natural history of fulgorids, and information describing interactions with host plants are particularly lacking. In our current study, we aimed to improve our understanding of how spotted lanternfly is attacking individual trees in the landscape. Our overall hypotheses are that spotted lanternfly exhibits nonrandom patterns in abundance, with increased attacks occurring on specific, individual trees in the landscape. Our specific objectives were to 1) evaluate the distribution and fidelity of spotted lanternfly attacks among individual trees over the late season; 2) evaluate timing of late-season movement onto new hosts and the potential spread into new areas; and 3) test whether spotted lanternfly attraction to particular trees is related to tree foliar mineral content. In order accomplish these objectives, we established multiple study sites in southeastern Pennsylvania over 2 yr where we evaluated spotted lanternfly attack on maple trees.

Methods

Site Locations and Descriptions

Over the course of the 2018 and 2019 field seasons we established five independent sites to address the distribution and constancy of spotted lanternfly attacks among individual trees over the season. All sites were established in southeastern Pennsylvania. We initially established field sites in areas that had reports of high spotted lanternfly adult abundance in the year prior. Each site was separated by at least 20 km. We used maples as focal species to evaluate spotted lanternfly tree-to-tree abundance at all sites although tree species composition differed between sites (Table 1). Some locations were entirely red maple (*Acer rubrum*; Topton [To], Wyomissing [Wy], Douglasville [Dv], Colony [Co]) and one site was composed of red maple and silver maple (*Acer saccharinum*; Wethersfield [Wf]). Trees sampled at each site were established from transplants from several seasons to two decades old, exhibited no signs of injury or decline, were evenly spaced, and were approximately the same size and age at each location. Trees at To and Dv were along a roadway, those at Wy and Co were in a residential neighborhood, and those at Wf were in an open park-like setting. For all sites and in both years, adult spotted lanternfly began to attack maples in late August and

Table 1. Summary of sites and sampling details for time-course evaluation of spotted lanternfly tree colonization

Site	Year	Sampling frequency	Sampling method	Sample size	Focal tree species
Douglasville (Dv)	2018	3–4 d	Dead counts	12	Red maple
Topton (To)	2018	1–2 wk	Live tree counts	40	Red maple
Weathersfield (Wf)	2019	2 wk	Live tree counts	45	Red and silver maple
Colony (Co)	2019	2 wk	Live tree counts	42	Red maple
Wyomissing (Wy)	2019	Weekly	Live tree counts	20	Red maple

early September and continued to feed on trees until a hard freeze in both years. Connectivity to rural and forested landscapes differed between the sites, but those impacts are outside the scope of our current study.

We used the sites in 2018 to establish the sampling parameters and initially determine attack success and determined sampling needed to occur for the duration of September and October (see Results section). We then established three additional sites in 2019 to perform sampling throughout the fall until hard freeze. Due to site restrictions and other research objectives implemented at these sites, sampling frequency, method to enumerate spotted lanternfly adults, and duration of sampling varied (Table 1).

Determining Patterns and Duration of Spotted Lanternfly Attacks

In 2018, we established a lower branch count metric as a way of estimating spotted lanternfly abundance, where we count spotted lanternfly present on lower branches (≤3 m) abundances as a metric for estimating spotted lanternfly adult numbers on each tree. We validated this metric at our Dv site (see Supp Fig. 1 [online only]). These trees were relatively even-aged new transplants planted at the same time with similarly sized crowns. At Dv, the number of spotted lanternfly adults were counted from the base of the tree up to 3 m, then were counted along the branches in a 3-m diameter along the lower tree crown. After enumerating live adults, trees were injected with the highest label rates of dinotefuran (Mauget Dinocide HP 12% Active Ingredient), using an Arborjet quick jet air and #4 (3/8″) arbor plugs at a rate of 2 ml of Dinocide per inch of tree DBH with plugs placed approximately at every 6″ of circumference. We returned to the trees 2 d after insecticide application and collected dead insects from tarps. Analysis of lower branch counts confirmed these to be a good estimator of total abundance (see Results; Supp Fig. 1 [online only]) and this approach was subsequently used as a method to repeatedly sample population abundances at our other sites.

Initial site scouting determined few spotted lanternfly nymphs were present on the maple trees at our sites prior to August in both 2018 (C.J.M., B.W., J.M.U., personal observations) and 2019 (Supp Fig. 1 [online only]). In 2018, population estimates were determined from dead adults collected from tarps deployed at the Dv site, where samples were collected every 3–4 d from late August to early October. At the 2018 To site, we used lower branch count methodology to evaluate the tree abundance from late August to early October every week. In 2019, we exclusively used the lower branch counts at all three sites (Wf, Co, and Wy). At Wf and Co sites, live adult spotted lanternfly estimates were determined on a biweekly sampling basis from late August to November. At the Wy site, estimates were conducted on a weekly basis from late August to November. Additionally, we also recorded the number ratio of male:female spotted lanternfly that were colonizing trees at the Wy site. Sex ratios were not determined at the other sites. Live spotted lanternfly were enumerated on each tree at each site using this standardized method in the late morning or early afternoon. In order to minimize individual sampling biases, the counts were performed by one individual at all trees at a site for each time period.

Relationships Between Spotted Lanternfly Abundance and Tree Foliar Mineral Content

In order to evaluate if variation in tree nutrition may contribute to spotted lanternfly attack patterns, we investigated whether spotted lanternfly counts on trees were correlated with the elemental composition of tree foliage. At the Dv and Wy sites, we evaluated spotted lanternfly abundance on individual trees for 12 and 16 trees, respectively, in September 2019. Spotted lanternfly abundances on trees were estimated using the lower branch count method. For samples taken, we identified trees that exhibited a range in abundances from 0 to >200 (Supp Table 1 [online only]). Immediately after counts were enumerated, we used pole pruners to remove foliage from the middle of the outer tree canopy from each of the four cardinal directions. A minimum of seven leaves from each section were removed from stems, pooled, transported to the laboratory on ice, and dried in an oven at 60°C for 48 h. Leaves were then ground in a Wiley mill until it was able to be passed through a 1-mm^2 mesh. Quantification of foliar elemental composition (N, P, K, Ca, Mg, Mn, Fe, Cu, B, Al, Zn, Na, and S) was completed at the Pennsylvania State University Ag Analytical Services Lab using acid digestion following standard protocols.

Statistical Analyses

Initial analysis of our data indicated that spotted lanternfly abundance varied over time of sampling and across individual trees where sampling was conducted (see Results). The core hypothesis we tested was that individual maples within any site supported higher abundances of spotted lanternfly as compared to other individual trees. Given the different sampling methodologies, frequencies, and durations (Table 1), we opted to analyze each site's data separately. We used nonparametric Freidman tests as our primary method of data analysis to determine if individual trees consistently ranked higher in spotted lanternfly abundance than other trees at the same location over time. Following the main test, we performed post hoc Nemenyi tests to determine pairwise differences between individual trees. Friedman tests and post hoc analyses were performed in the R-studio v.1.2.5033 environment using R v.3.6.3 (R Core Team 2020).

In order to evaluate how foliar minerals may be related to spotted lanternfly attack abundances, we used partial least squares regression (PLSR) (Wold et al. 1984). PLSR jointly transforms predictor and response variables to identify orthogonal latent vectors that maximize explanation of covariance within a data matrix (Singh et al. 2015). PLSR is designed for analyses in which sample size may be low relative to number of independent variables or in which independent variables may be highly correlated, both of which apply to this data set (Carrascal et al. 2009). We used PLSR rather than model selection because it enables comparisons among dependent variables as all potential independent variables are retained in the analysis (Grossman et al. 1996). We included data across the two sampling sites and used elemental composition as predictors of spotted lanternfly abundance. In order to achieve consistent response variables, spotted lanternfly counts at each location were standardized by setting the tree with the highest abundance at 1.0, and all other counts were then relativized to the peak abundance. Mineral data were standardized and centered before the analysis. We identified the optimal number of latent variables using leave-one-out cross-validation and selected them based on the reduction of the predicted residual error sums of squares (PRESS) statistic. After identifying the optimal number of latent variables (in this case two), we employed the variable importance of projection statistic (VIP, a weighted measure based on absolute coefficient size and partial-R^2 of a predictor (Wold 1994)) to assess the importance of the individual predictor variables on spotted lanternfly densities, using 0.8 as a cutoff for retaining variables in the model. Following initial model building and variable selection, we randomly withheld 30% of the sampling data for external model validation and refitted the PLSR model with only the VIP selected predictors. PLSR was performed in JMP v 14.0.

Results

Late-Season Movement of Adult Spotted Lanternfly Onto Ornamental Trees

While spotted lanternfly has the capacity to feed on diverse food sources across its life span (i.e., herbaceous plants, woody plants, and trees), anecdotal evidence suggested that they feed in high numbers on trees with ornamental value, particularly late in their development. Our data obtained across multiple sites and the 2018 and 2019 field seasons support these observations (Fig. 1). In all sites we studied, there were generally fewer adult spotted lanternfly in late August and into early September despite being well into adult maturation.

Peak abundances were generally observed at the beginning of October for our study region (Fig. 1). While we did observe egg masses from the previous years, we typically did not observe high abundances of nymphs or adults prior to our surveys (July) that would suggest complete development on a given tree (Supp Fig. 2 [online only]). Rather, movement from the surrounding landscape and attacking new trees appears to be how spotted lanternfly operates in these environments. This movement is further evidenced by our data obtained at Dv, where a systemic insecticide was used as a sampling measure and some of the trees still harbored high proportions of spotted lanternfly. In 2018, we observed differences between the timing To and Dv population peaks, but sampling was terminated early. In 2019, there seemed to be greater synchrony in the spotted lanternfly abundances across the Co, Wf, and Dv sites (Fig. 1), but population densities differed from other sites that we sampled (Supp Fig. 2 [online only]).

At Wy, we observed earlier movement of males from the surrounding landscape onto maples prior to female movement (Fig. 2). The first arriving adults were almost entirely male. As attack densities increased (Fig. 1), the ratio became closer to even. Late in the season, the ratio was much more female-biased.

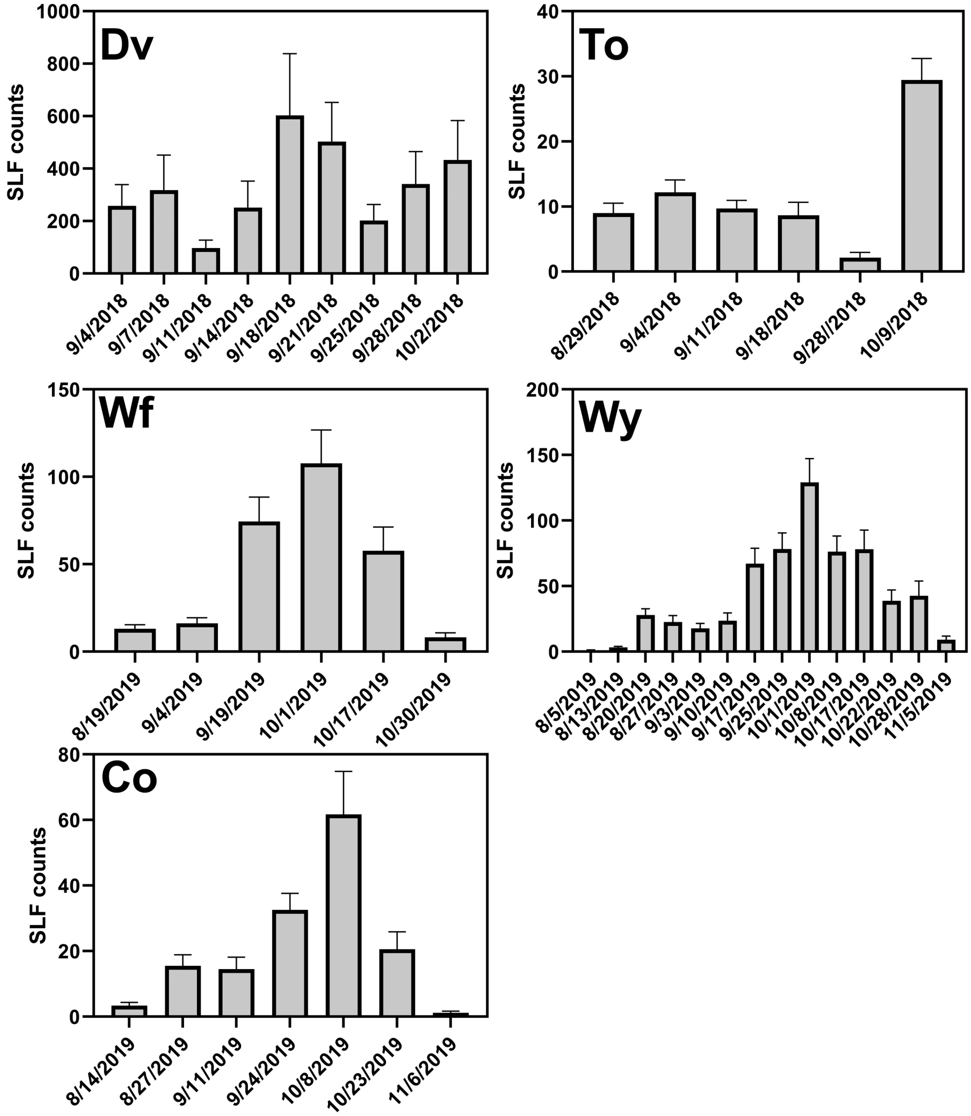

Fig. 1. Timing spotted lanternfly adult colonization of maples through August–September. Site abbreviations, descriptions, and methods are provided in Table 1. Bars represent means + 1 SE. Numbers of spotted lanternfly were either collected from insecticide-treated plants (Dv) or counted along lower sections of the tree (To, Wf, Wy, Co). Silver maple comprised all of trees sampled at Dv, red maple at To, Wy, and Co, and a mixture of the two are included in Wf. Additional sites showing other populations are provided in Supp Fig. 2 (online only).

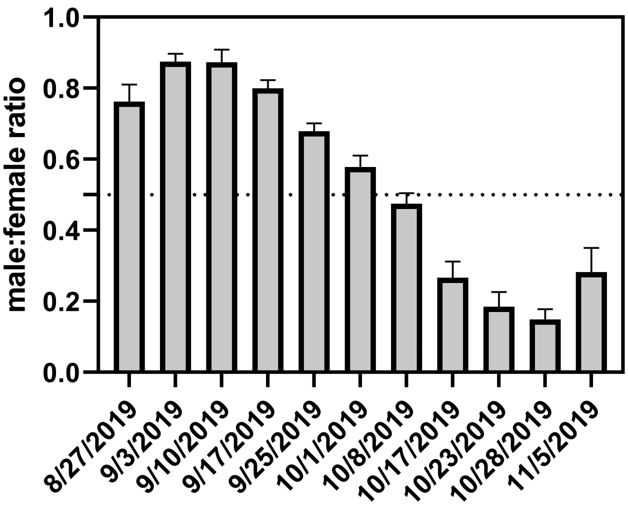

Fig. 2. Ratio of males–female at Wyomissing. Bars represent mean ratio per tree (+SE). Dotted line indicates equal ratios of male–female spotted lanternfly.

Impact of Individual Trees on Spotted Lanternfly Abundance

We observed considerable tree-to-tree variation in spotted lanternfly attack densities across our sites (Fig. 3). At all our sites across both seasons, we observed significant effects of the individual host tree in influencing spotted lanternfly attack numbers, and this effect was consistent throughout the season (Fig. 4). In some instances, trees had consistently greater numbers of spotted lanternfly while others exhibited far lower abundances. The overall effect of an individual tree in influencing spotted lanternfly attack was statistically significant across all sites (Dv: $\chi^2_{11} = 81.2$, $P < 0.001$; To: $\chi^2_{39} = 127.4$, $P < 0.001$; Co: $\chi^2_{41} = 97.6$, $P < 0.001$; Wf: $\chi^2_{44} = 123.2$, $P < 0.001$; Wy: $\chi^2_{19} = 128.7$, $P < 0.001$). This pattern is apparently robust given the different sampling methodologies, durations, and frequencies that we employed in our study.

When we conducted pairwise comparisons between trees within each site, we observed some significant differences between individual trees. In general, highest incidences of pairwise differences were observed for the Dv and Wy sites, where pairwise comparisons revealed that there was a clear separation in rank abundance of spotted lanternfly across the season for half of the trees at both sites. Fewer significant pairwise comparisons were present for the To and Wf sites, where differences were primarily present for trees that had either the highest spotted lanternfly densities or the lowest. We did not observe significant pairwise comparisons for the Co site. The Co site exhibited greater variation in tree rank than the other sites throughout the season, and particularly at the lower spotted lanternfly densities (Figs. 3 and 4). All pairwise comparisons are reported in Supp Table 2 (online only).

Influence of Tree Elemental Composition as a Predictor of Spotted Lanternfly Abundance

We used foliar elemental composition as a proxy for evaluating whether there were components of the maples that would facilitate spotted lanternfly congregation at a single timepoint. Our calibration model, used for variable selection, explained 55% of the variation in spotted lanternfly abundance in early October 2019 (Fig. 5A). When we performed external validation using the including only foliar mineral content selected by VIP on a random subset of samples (Table 2), the model improved to explain 63% of the variation (Fig. 5B). These results suggest robust support for host plants nutrient quality shaping spotted lanternfly attack densities at a given point in time. Foliar nitrogen, calcium, and sulfur concentrations all had positive relationships with spotted lanternfly attack, while phosphorous, potassium, iron, and sodium had negative relationships with spotted lanternfly attack.

Discussion

Multiple environmental factors can influence host plant colonization by insect herbivores. Herbivorous insects must locate and exploit suitable host plants that provide nutrients for physiological maintenance and, ultimately, production of offspring. While spotted lanternfly can exploit a diversity of food resources, the feeding preferences of nymphs and adults shift through development. Our data provide support to the notion that there is a late-season movement of adult insects from the surrounding landscape to select, specific maple trees. Current governmental (USDA and state departments of agriculture) efforts aimed to reduce adult spotted lanternfly populations largely target tree of heaven. Our data across multiple years and sites document that red maple harbors high numbers of late-season adult spotted lanternfly and therefore may represent an additional window of opportunity for additional control measures.

Our data also suggest that attacks are not random, and that plants that harbor large numbers of adults generally maintain elevated spotted lanternfly abundance throughout the season. Moreover, we show that variation in tree foliar elemental composition covaried with the number of spotted lanternfly colonizing trees. There are several major takeaways from our results that have implications to how this herbivore exploits tree hosts. First, movement of adult spotted lanternfly from surrounding areas onto ornamental red and silver maple occurs relatively late in the season, and different movement periods potentially occur for the different sexes. Second, spotted lanternfly tends to consistently attack specific trees in the landscape. Finally, variation in tree quality may drive the fine-scale patterns in attack. All three of these findings have the potential to inform targeted and effective management for this pest.

Identifying and exploiting suitable host plants is critical for insect herbivores, and colonization patterns can be impacted by environmental attributes. Locating hosts that are simultaneously nutritious and poorly defended is important for attack success. This is especially the case for phloem-feeding insects, where the benefits of evading plants' antiherbivore responses and exploiting higher nutritional quality trees can lead to increased attack and higher localized populations (McClure 1991, Kytö et al. 1996, Joseph et al. 2011). Multiple cues undoubtedly contribute to the selection of host plants by insect herbivores. Visual inspection, volatile emissions, conspecific communication, and the active feeding on plant substrates can all influence attraction to specific hosts. Movement from host plants is likely influenced by a decline in quality coupled with availability of better hosts in the landscape. At one of our sites, we observed the movement of males prior to the movement of females to new hosts, but the mechanism underlying that difference is unknown.

Currently, we do not know the principal signals that drive spotted lanternfly movement among various plants. Specific components of the tree of heaven and grape volatile blends have been suggested to function as potential kairomones (Cooperband et al. 2019), but we do not know how they impact the distribution of spotted lanternfly densities over the maple trees we observed. Fertilization can alter volatile profiles of other plant species (Gouinguené and

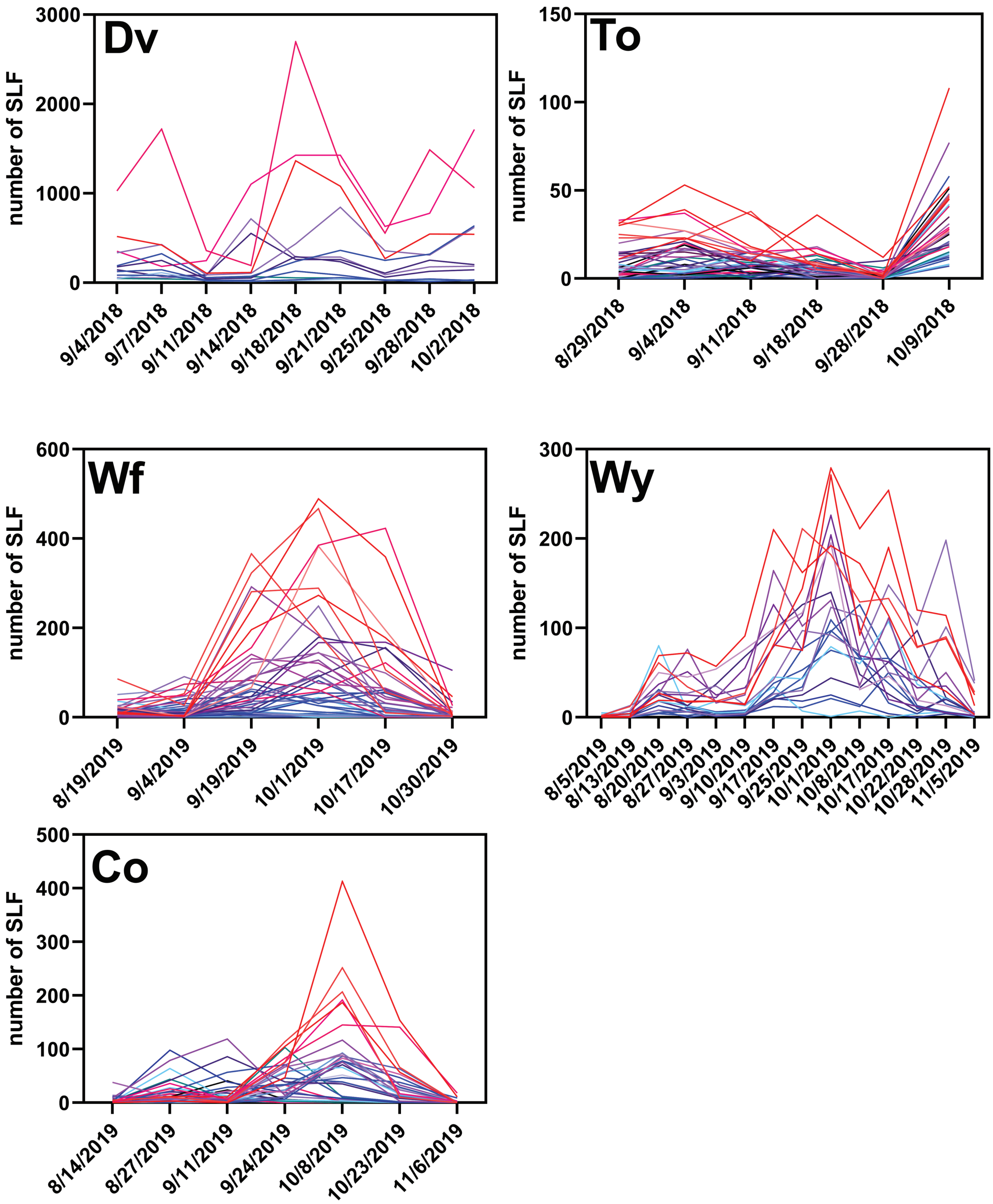

Fig. 3. Patterns of spotted lanternfly adult colonization of maples through August–September. Site abbreviations, descriptions, and methods are provided in Table 1. Each line follows colonization patterns of a single tree though the sampling period. Numbers of spotted lanternfly were either collected from insecticide-treated plants (Dv) or counted along lower sections of the tree (To, Wf, Wy, Co). Silver maple comprised all of trees sampled at Dv, red maple at To, Wy, and Co, and a mixture of the two are included in Wf.

Turlings 2002, Hu et al. 2018, De Lange and Rodriguez-Saona 2019), but we do not know if that phenomenon occurred in the current study. As an alternative, visual inspection of host plants, either though foliage or accumulation of conspecifics, may also be a contributing factor (Prokopy and Owens 1983, Reeves 2011). Probing behavior is common among other piercing-sucking insects as a mechanism of identifying superior hosts (Nowak and Komor 2010, Cao et al. 2018), and likely aids spotted lanternfly in the identification of superior and inferior substrates as well. Finally, while phenolic compounds in maples are known to act as defenses against folivorous insect herbivores (Barbehenn et al. 2005) and exist in the vasculature tissue of many trees (Smith 1997) and can influence sap-feeding insects (Grayer et al. 1992), we do not know how these defenses influence spotted lanternfly performance. Spotted lanternfly can consume host plants including tree of heaven and black walnut, which possess metabolites that exhibit high toxicity in other insects (Lidert et al. 1987, Thiboldeaux et al. 1994), suggesting that spotted lanternfly has some tolerance to plant defenses.

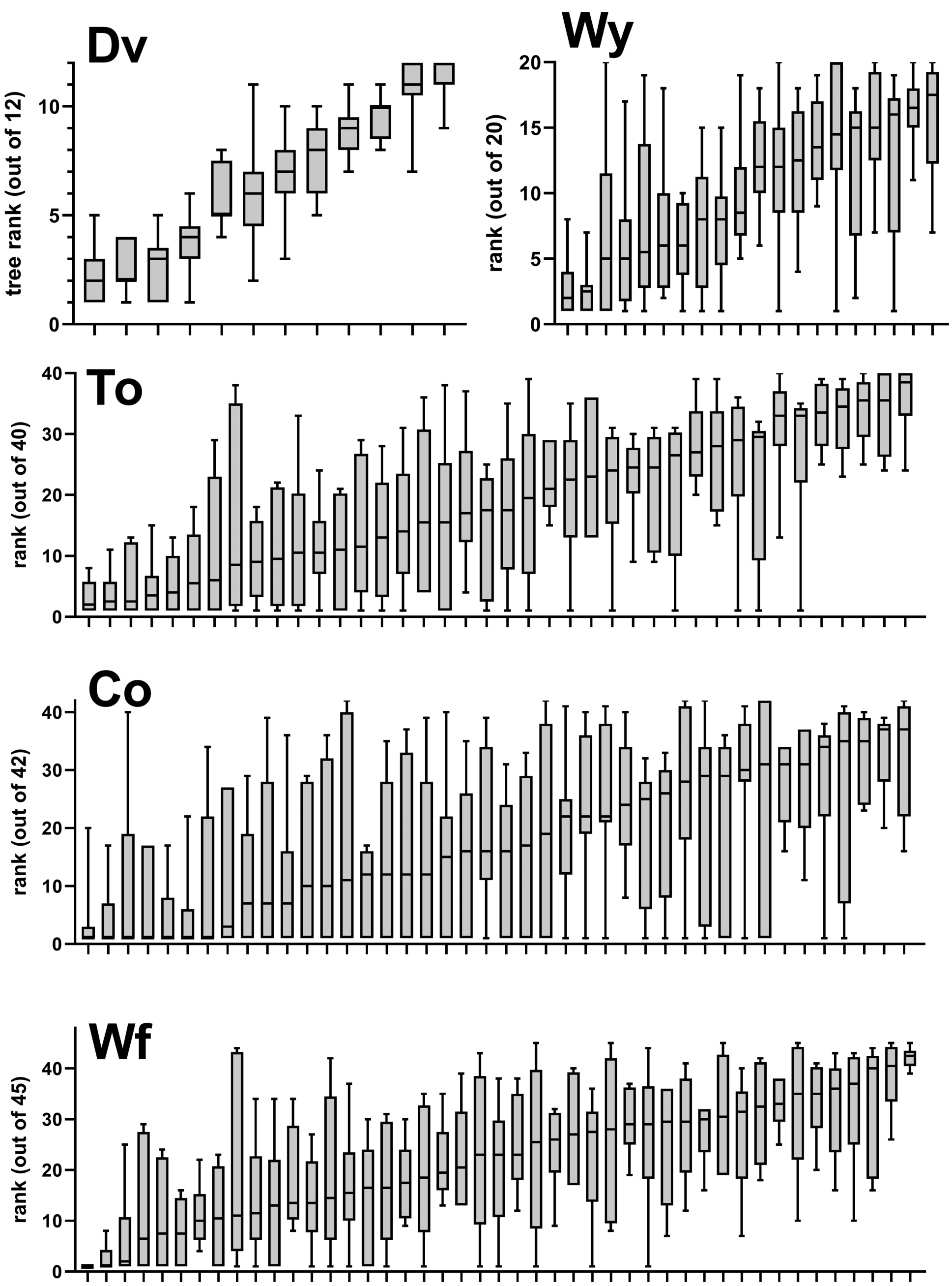

Fig. 4. Patterns of spotted lanternfly adult colonization as a function of rank through the season. Each boxplot represents an individual tree throughout the sampling period. A higher rank indicates that a tree had greater numbers of spotted lanternfly present at each sampling timepoint. Effectively, a lower rank indicates that a tree was generally the least colonized over the course of the season. Boxplots represent 25 and 75% quartiles, whiskers show range, and solid lines indicate medians. Site abbreviations, descriptions, and methods are provided in Table 1. Numbers of spotted lanternfly were either collected from insecticide-treated plants (Dv) or counted along lower sections of the tree (To, Wf, Wy, Co). Silver maple comprised all of trees sampled at Dv, red maple at To, Wy, and Co, and a mixture of the two are included in Wf. Pairwise comparisons of each tree as it relates to spotted lanternfly attack are present in the Supp Information (online only).

Links between foliar mineral composition and spotted lanternfly abundance suggest the insect is identifying and exploiting superior hosts in the landscape. While we should only consider foliage as a proxy of tree suitability, the positive relationships between spotted lanternfly abundance and some of the minerals we report have been previously observed in other systems. Plants high in nitrogen, generally considered the rate-limiting nutrient for insect growth and development (Mattson 1980), are frequently more attractive and support greater numbers of sap-feeding insects (Sōgawa 1982, White 1984, Rashid et al. 2017). Contrastingly, potassium can have a negative effect on herbivore performance (Myers and Gratton 2006, Rashid et al. 2017). Higher sodium levels corresponded to lower spotted lanternfly abundances, and sodium stress has been reported to negatively affect herbivore abundance (Sienkiewicz-Paderewska et al. 2017). The roles of calcium, sulfur, and iron in herbivore attraction and performance are unclear. Additionally, other factors apart from tree nutritional status can influence herbivore host selection. As high abundances

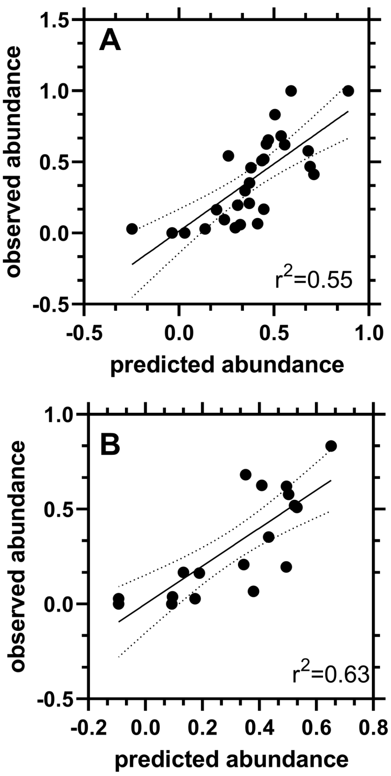

Fig. 5. Validation of models relating the predicted spotted lanternfly abundance on a given tree against the observed relative abundance using all data for variable selection (A) and a 30% holdback of the data for external validation (B). Models were constructed using partial least squares regression using foliar elemental composition as predictors.

of spotted lanternfly on maples occur late in the season, the insects are confronted by rapid changes in tree nutritional dynamics due to the onset of senescence (Keskitalo et al. 2005). Integration of host plant physiological responses and available nutrition would facilitate parsing of spotted lanternfly attraction, and enable better predictions of movement in the landscape.

A limitation in our elemental analysis is we did not sample trees prior to infestation, so we do not know what changes in tree physiology may have occurred after the onset of spotted lanternfly feeding. Sap-feeding insects have well-documented, direct impacts on plant physiology and nutritional status (Zvereva et al. 2010). Moreover, insect outbreaks can stress and deplete plant resources, and repeated feeding can significant damage and potential mortality in long-lived plants (Kosola et al. 2001, Hudgeons et al. 2007, Gonda-King et al. 2014). In light of the apparent spotted lanternfly-induced mortality observed in grape (Urban 2020), identifying immediate and long-term impacts to tree health in future work is critical.

Management of spotted lanternfly is hindered by numerous challenges. The pest is difficult to detect at low densities, feeds on a variety of hosts, and has different periods of movement to new resources. A more complete understanding of the factors driving the seasonal timing and orientation of spotted lanternfly movement needed to improve the effectiveness of management. Our data show that there are late-season influxes of spotted lanternfly on ornamentals, but variable attacks on individual trees suggest a prophylactic application strategy would result in treating trees with insecticides that may not ultimately support high densities. There are clear trade-offs in costs and potential nontarget effects for the management of spotted lanternfly in urban and suburban settings, and more refined management plans are needed to contend with this insect as it moves across forested, urban, suburban, and agricultural habitats. Ultimately, for areas experiencing outbreaks of spotted lanternfly, there should be an expectation for late-season movement on to trees that had not had high populations earlier in the season. However, currently we do not know how year-to-year variation may impact movement into suburban landscape, or how regional population dynamics and movement changes these relationships.

Table 2. Standardized coefficients calculated using partial least squares regression analysis relating maple foliar elemental composition to spotted lanternfly abundance

Foliar elemental variable	Effect on spotted lanternfly abundance
Nitrogen	0.5014
Phosphorus	−0.3984
Potassium	−0.3157
Calcium	0.4509
Sulfur	0.0823
Iron	−0.3805
Sodium	−0.1185

Predictor variables retained in the final model were selected using a cutoff of the VIP statistic of 0.8. Positive or negative weighted coefficients indicate positive or negative effects, respectively, on predicted spotted lanternfly abundance on a given tree. Effects sizes are conducted with centered and standardized data.

Our data provide evidence that spotted lanternfly undergoes a late-season movement period and has varying degrees of fidelity to ornamental maples. Collectively, our results support anecdotal reports describing high fidelity to individual host plants in spotted lanternfly and other fulgorids (Hogue 1984, O'Brien 2002), yet many knowledge gaps remain regarding spotted lanternfly plant exploitation. For example, better connections between the spotted lanternfly attack patterns to mechanisms of attraction are needed. Information on how spotted lanternfly are altering plant physiology immediately and under longer-term infestation is also lacking. Accurate predictions of spotted lanternfly abundance demand improved information on the locations of reservoir populations and improved understanding of how landscape connectivity affects movement. Finally, clarity on the nutritional needs of spotted lanternfly along with how those requirements change through the season and across host plants, would enable a more robust understanding of how spotted lanternfly is determining quality hosts.

Supplementary Data

Supplementary data are available at *Environmental Entomology* online.

Supp Fig. 1. Relationship between lower branch SLF counts and the number killed two days after dinotefuran treatment.

Supp Fig. 2. Different sites have different SLF abundances numbers and population peaks. Numbers are a two-week average across the site to enable consistent comparisons. Values represent average number per tree at each interval.

Supp Table 1. Raw data for evaluating SLF counts related to foliage elemental contents.

Suppl Table 2. Post hoc Nemenyi tests comparing individual tree attack frequencies.

Data Accessibility

We will deposit data on which analyses were based upon acceptance of our manuscript. Raw data have been deposited at doi:10.6084/m9.figshare.12902576.

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